ANNALS OF CARNEGIE MUSEUM
VOL. 70, NUMBER 3, PP. 221–230 17 AUGUST 2001

MIDDLE EOCENE ISCHYROMYIDAE (MAMMALIA: RODENTIA) FROM THE SHANGHUANG FISSURES, SOUTHEASTERN CHINA

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ABSTRACT

Ischyromyid rodents from Middle Eocene fissure fillings in the Shanghuang Quarry, Jiangsu Province, include *Anatoparamys crepaturus*, n.g. and sp., and four other, probably allied taxa. These rodents appear to represent an endemic lineage of Asian rodents that are derived in the direction of bunodont, non-lophate cheek teeth, suggesting a preference for a diet of soft vegetable matter.

KEY WORDS: Middle Eocene, ischyromyid rodents, Asian endemism

INTRODUCTION

The Ischyromyidae, members of one of the oldest known and most primitive families of rodents, have a Holarctic Paleogene distribution (Wood, 1962; Michaux, 1968; Black, 1968, 1971; Dawson, 1977; Korth, 1984; Ivy, 1990; Escarguel, 1999). The family is prominent in North America, but relatively rare in both Europe and Asia. Although reports of Ischyromyidae or Paramyidae from the Paleogene of Asia are not uncommon (for example, Li, 1963, 1975; Dawson, 1964, 1968; Sahni and Khare, 1973; Sahni and Srivastava, 1977; Hussain et al., 1978; Li et al., 1979; Bruijn et al., 1982; Shevyreva, 1984; Qi, 1987), a number of these taxa actually belong to other families, especially within the Ctenodactyloidea, not to the Ischyromyidae (Dawson, 1977; Wood, 1977; Hartenberger, 1982; Dawson et al., 1984; Tong, 1997).

To date, five moderately well-defined ischyromyid species can be recognized in the Asian Eocene, *Hulgana ertnia, Eoischyromys youngi, Asiomys dawsoni, Taishanomys changlensis*, and *Acritoparamys? wutui*. Of these *Hulgana* is a relatively derived ischyromyid known by several upper and lower jaws from the Late Eocene Ulan Gochu Formation of Inner Mongolia (Dawson, 1968). *Eoischyromys* is a late or latest Middle Eocene rodent recognized from one jaw collected in the Changxindian Formation of northern China and one from the upper red beds (?Shara Murun Formation) of Inner Mongolia (Wang et al., 1998). *Asiomys* is based on three isolated teeth from the Middle Eocene Arshanto fauna of Inner Mongolia (Qi, 1987). *Taishanomys* and *Acritoparamys? wutui* are each represented by a lower jaw with molar teeth from the Wutu Formation of Shandong Province (Tong and Dawson, 1995). Two other named taxa, *Paramys obayliensis* and *Abrosomys agasma*, are each known from one isolated tooth and will not be considered further here due to their sparse record (Shevyreva, 1984). The

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Submitted 23 January 2001.

same is true of some isolated ischyromyid teeth that have been described from the Middle and Late Eocene of Inner Mongolia (Li, 1963; Dawson, 1964).

The fossiliferous fissure fillings in Shanghuang Quarry (Triassic Shangqinglong limestone), near Shanghuang village in southern Jiangsu Province, have produced a diverse record of Paleogene mammals (Qi et al., 1991, 1996; Wang and Dawson, 1994; Qi and Beard, 1996). Among them, ischyromyid rodents were collected from four of the five fissures (IVPP localities 93006.A [fissure A], 93006.B [fissure B], 93006.D [fissure D], and 93006.E [fissure E]) from which collections were made by quarrying followed by screen washing. Correlation based on the mammalian assemblages suggests an Irdinmanhan to early Sharamurunian Asian Land Mammal Age (ALMA) for the fissures, with fissure 93006.B being slightly younger than fissures 93006.D and E. All of the currently known ischyromyids are represented only by isolated teeth. At least four and possibly five taxa appear to be present. Even this incomplete record is of importance, due both to the general rarity of ischyromyids in the Asian Paleogene and to insights that these rodents can provide on their phylogenetic and geographic affinities.

METHODS

Biochronologic terminology for Paleogene localities in China follows Tong et al. (1995). Worldwide correlations are based on Berggren and Prothero (1992). Abbreviation for repository: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Ischyromyidae Alston, 1876

Anatoparamys crepaturus, **new genus and species**

Holotype.—Right M_2, IVPP V 11032.1.

Referred specimens.—Three right dP_4 (V 11032.3, V 11035.1, V 11035.2), right P_4 (V 11032.2), left M_1 (V 11032.4), right $M_{1 \text{ or } 2}$ (V 11032.5, V 11032.6, V 11032.16), left M_3 (V 11032.7), right dP^4 (V 11032.8), left dP^4 (V 11032.12), left P^4 (V 11032.9), right M^1 (V 11032.13), two right M^2 (V 11032.14, V 11032.15), two right M^3 (V 11032.10, V 11032.11).

Diagnosis.—Medium-sized ischyromyid (Table 1) having bunodont cheek teeth with rounded cusps and contours, very little development of lophs, which, where present, are narrow; upper cheek teeth have complete, narrow protoloph, protocone anteroposteriorly elongate, prominent rounded metaconule; protoconule absent and very little or no trace of a hypocone; P_4 elongate with narrow trigonid, small trigonid basin and protoconid; lower molars rhomboidal in shape, expanded anterolingually, trigonid basin small, talonid basin wide and shallow, entoconid very small and no trace of a hypolophid.

Differs from other ischyromyids in combination of the following characters: rounded cusps of all cheek teeth; anteroposteriorly elongate protocone of P^4–M^3; absence of hypolophid of lower cheek teeth; absence of protoconule and rudimentary or absent hypocone on upper cheek teeth; rhomboidal shape of lower molars.

Localities.—Fissure D (V 11032); fissure E (11035).

Etymology.—Greek, *anatole*, east, and *Paramys*, a well-known genus of Paleogene ischyromyid; Latin, *crepatura*, fissure.

Table 1.—*Measurements (in mm.) of Shanghuang Ischyromyidae (all numbers are preceded by IVPP V).*

Number	Locus	Anteroposterior	Transverse
Anatoparamys crepaturus			
11032.8	dP^4	3.10	3.50
11032.9	P^4	3.0	3.93
11032.13	M^1	3.66	4.12
11032.14	M^2	3.59	4.40
11032.10	M^3	3.60	3.70
11032.11	M^3	3.50	3.50
11032.3	dP_4	3.40	2.90
11035.1	dP_4	3.50	2.95
11035.2	dP_4	3.45	2.90
11032.2	P_4	4.0	3.3
11032.4	M_1	3.6	3.75
11032.5	M_1	3.75	3.90
11032.6	M_1	3.90	4.0
11032.1	M_2 (holotype)	4.0	4.0
11032.7	M_3	4.0	3.6
Anatoparamys sp.			
11033.3	dP_4	3.12	2.7
11034	P_4	3.4	3.5
11033.2	M_3	3.28	3.19
ischyromyid taxon 1			
11037.1	dP^4	3.52	3.56
11037.2	M^2	3.46	3.86
ischyromyid taxon 2			
11036.1	$M^{1 \text{ or } 2}$	4.30	5.50
11036.2	M^2	5.30	6.70

Description.—The isolated cheek teeth by which this new taxon is known are distinctly bunodont, with rounded outlines and cusps and little development of lophs. Two small buccal roots and one strong lingual root support the upper molars. The lower permanent cheek teeth have two strong, sturdy roots, one each under the trigonid and the talonid. The trigonid root of M_3 has two pulp cavities. Lingual enamel on the permanent upper teeth extends farther up the tooth shaft than the buccal enamel, suggesting some lingual hypsodonty.

P^4 (Fig. 1B) is a transversely wide tooth. Its most striking feature is the anteroposteriorly elongated, obliquely set protocone, which fills the lingual side of the tooth. There is no hypocone. Paracone and metacone are well developed cusps, and the metaconule is also strong. The paracone is extended lingually by a short protoloph, and the metacone by a metaloph that connects to the metaconule. In this relatively little worn tooth there is no loph from metaconule to protocone. The anterior and posterior cingula are strong transverse ridges.

The three $M^{1 \text{ or } 2}$ referred here may represent both loci, the one interpreted as M^1 being transversely narrower but anteroposteriorly longer than the probable M^2 (Fig. 1C). These molars have an elongate protocone with little or no trace of any hypocone swelling, a straight complete protoloph between paracone and protocone, and a distinct, rounded metaconule. In the less worn teeth, there is no connection between the metaconule and the protocone, but a connection may develop following greater wear. M^1 has a rounded mesostyle and a small, rounded cuspule buccal to the metaconule. The more worn M^2 have an elongate mesostyle and lack a discrete second metaconule.

One little worn (Fig. 1D) and one worn specimen of M^3 share with the other upper teeth an anteroposteriorly elongated protocone. The protoloph extends to the protocone. The metaconule is very small and isolated on the less worn tooth (V 11032.11), whereas in the more worn tooth (V 11032.10) it connects to an indistinct metacone via a metaloph. M^3 increases in area of the occlusal surface as it wears down, so the more worn tooth appears to be the larger of the two.

Both upper and lower deciduous teeth have been referred to this taxon. Association of two specimens of dP^4 (Fig. 1A) with *Anatoparamys* is supported by the similarly large, elongate and oblique protocone

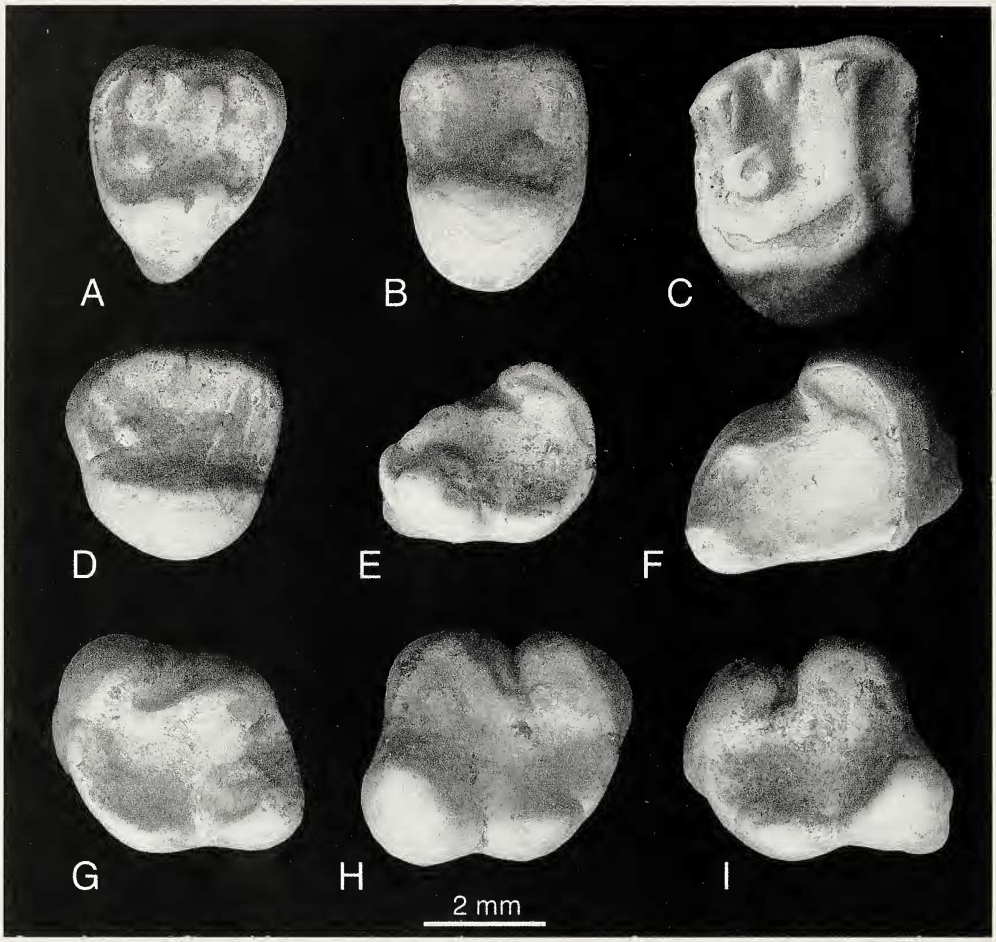

Fig. 1.—Occlusal views of cheek teeth of *Anatoparamys crepaturus*. A. Right dP^4, IVPP V 11032.8. B. Left P^4, IVPP V 11032.9. C. Right M^2, IVPP V 11032.14. D. Right M^3, IVPP V 11032.11. E. Right dP_4, 11032.3. F. Right P_4, IVPP V 11032.2. G. Left M_1, IVPP V 11032.4. H. Right M_2, IVPP V 11032.1, holotype. I. Left M_3, IVPP V 11032.7.

that they share with P^4. These teeth are expanded anterobuccally by a distinct cingular shelf. The metaconule is well rounded.

The only known P_4 (Fig. 1F) is slightly broken, lacking some enamel on the lingual and anterior surfaces. It is an elongate tooth, having a long wear facet anterior to the posterior arm of the protoconid. The protoconid is low, the metaconid is the highest cusp and is in a line anterior to the protoconid. A narrow posterior arm of the protoconid extends obliquely forward to the metaconid. The narrow, complete ectolophid lacks any trace of a mesoconid. The large hypoconid protrudes anteriorly; posterolingually it extends directly into the curved posterior cingulid. There is no trace of an entoconid, possibly due to lingual damage to the specimen, or of a hypolophid, a real absence. The talonid basin is wide and shallow.

The lower molars are rhomboidal in shape, with a lingually protruding metaconid. This shape is least well developed on M_1 (Fig. 1G), more pronounced on M_2 (Fig. 1H), and most prominent on M_3 (Fig. 1I). The ectolophid of M_1 appears anteroposteriorly longer and transversely narrower, whereas those on the following two molars are shorter and wider, reflecting the more rounded protoconid on the latter two molars. On $M_{1\text{-}2}$ the posterior arm of the protoconid extends anterolingually to a comparable buccal ridge on the metaconid, forming a metalophid that closes posteriorly a very constricted

trigonid valley, which is bounded anteriorly by a well-developed anterior cingulum. On M_3 there is no buccal ridge on the metaconid and the trigonid basin is open posteriorly. A distinct notch occurs on the lingual side of the molars between metaconid and entoconid. The molar entoconids are plump and low and have no sign of loph development. The hypoconid-posterior cingulid-entoconid ridge is distinctly convex posteriorly, enclosing a somewhat elongated talonid valley. A slight indication of a hypoconulid is present on the posterior cingulid of M_1 but absent on M_{2-3}. The enamel in the talonid valley of M_3 is slightly wrinkled.

DP_4 (Fig. 1E) is an elongate tooth having the anterior occlusal surface formed by a ridge that curves from the protoconid to the anterobuccal surface of the metaconid. The metaconid is a tall, prominent cusp, whereas the protoconid is low and small. A low posterior arm of the protoconid extends obliquely forward to the metaconid; a short, low lophid that extends posteriorly from the posterior arm of the protoconid parallels a similar lophid from the posterolingual edge of the metaconid. The ectolophid is low and complete between protoconid and hypoconid. The hypoconid extends without break into the posterior cingulid, which is distinctly convex posteriorly. Only a tiny swelling suggests presence of an entoconid. Two dP_4 from fissure E are essentially identical to the one from D and are referred to this taxon.

Comparisons.— *Anatoparamys* is a distinctive ischyromyid in its markedly bunodont, nearly non-lophate cheek teeth. None of the previously known Asian Eocene ischyromyids have evolved this type of dentition. The Early Eocene ischyromyids *Taishanomys* and *Acritoparamys? wutui* are quite primitive but the former differs from *Anatoparamys* in having a long molar trigonid and the latter differs from it in having a very well-developed entoconid that is separated from the posterior cingulid. There is no clear indication from either of these more primitive rodents of close phylogenetic affiliation with *Anatoparamys*. The upper molar structure of the Middle Eocene *Asiomys*, having an anteroposteriorly short protocone and a distinct hypocone, clearly differentiates it from *Anatoparamys*. *Eoischyromys* of the latest middle Eocene of northern China is very different from *Anatoparamys* in having an anteroposteriorly short P_4 and molars with a strong posterior arm of the protoconid and a long complete hypolophid; it has been referred to the otherwise North American subfamily Ischyromyinae (Wang et al., 1998). The Late Eocene *Hulgana* is similar to *Anatoparamys* in lacking a distinct hypocone and a hypolophid, and having a slightly rhomboidal shape of the lower molars, and a wide, shallow talonid basin. Differently derived characters of *Hulgana* include its anterolingually protruding protocone, stronger lophs of the upper cheek teeth, and anteroposteriorly short P_4. Although *Anatoparamys* and *Hulgana* appear to be evolving in different directions, the morphological characters that they share could indicate relationship of both to an ischyromyid considerably earlier in the Eocene.

Among non-Asian ischyromyids, *Anatoparamys* shares some characteristics that could be indicative of relationships with the manitshine ischyromyids (Wood, 1962; Korth, 1985), which are mostly large, North American rodents having rounded cusps that are more dominant in the occlusal pattern than are the lophs. Some species of manitshines have a P_4 similar to that in *Anatoparamys* with a small protoconid and small trigonid basin, but this morphology is also found in several other relatively primitive ischyromyids such as *Franimys* and *Paramys copei* and cannot be relied upon to support phylogenetic relationships. The manitshines tend to have at least some development of a hypocone in the upper molars, a primitive ischyromyid feature, and a crest between the anterior side of the hypoconid and the entoconid, characters absent in *Anatoparamys*. The rhomboidal shape of the lower molars, found in *Anatoparamys*, is not strong or absent in manitshines.

Anatoparamys is a rodent that seems to be in the process of simplifying the

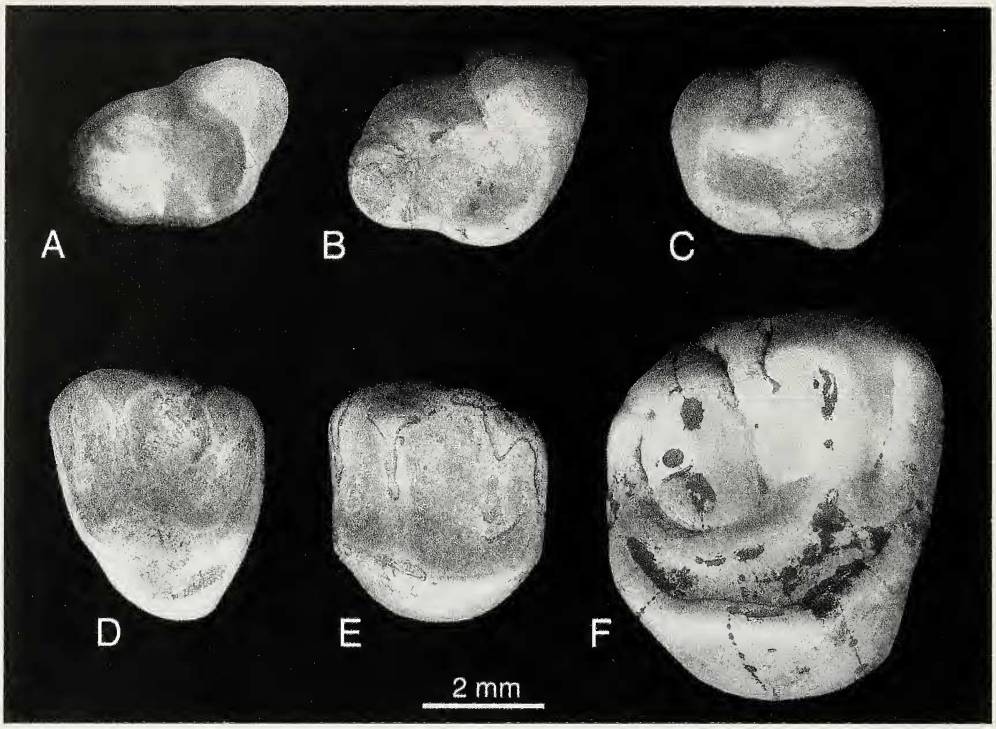

Fig. 2.—Occlusal views of cheek teeth of Shanghuang ischyromyids. A–C. *Anatoparamys* sp. A. Right dP_4, IVPP V 11033.3; B. Right P_4, IVPP V 11034; C. Left M_3, IVPP V 11033.2; D–E. Ischyromyidae taxon 1. D. Left dP^4, IVPP V 11037.1; E. Left $M^{1 \text{ or } 2}$, IVPP V 11037.2; F. Ischyromyidae taxon 2. Right M^2, IVPP V 11036.2.

occlusal surface of its cheek teeth while increasing its bunodonty. More primitive ischyromyids usually have more lophate cheek teeth and better-developed hypocone, protoconule, and entoconid (Tong and Dawson, 1995; Dawson and Beard, 1996). The simple, bunodont teeth of *Anatoparamys* appear to be adapted for chewing soft fruits and other vegetation.

Anatoparamys sp.

Specimens.—Right P_4 , IVPP V 11034; left P_4, V 11033.1; left M_3, V 11033.2; right dP_4, V 11033.3.

Localities.—Fissure D (V 11033), Fissure E (11034).

Description.—These four teeth are smaller than corresponding teeth assigned to *Anatoparamys crepaturus* (Table 1) and, while similar in having rounded cusps and weak lophs, are also morphologically different from that species. Their generic association seems likely, although the small number of specimens does not allow for certainty in this assignment.

On the trigonid of P_4 (Fig. 2B) the metaconid is a very prominent, rounded cusp, larger relative to the protoconid than in *A. crepaturus*. It differs also from the P_4 of *A. crepaturus* in having the trigonid that is less elongated anteriorly and has an even smaller trigonid basin, which is little more than an open notch between protoconid and metaconid. M_3 (Fig. 2C) differs from that of *A. crepaturus* in having a less rhomboidal shape, related to the talonid not being expanded posterobuccally. The anterior cingulid of M_3 is relatively farther forward than in *A. crepaturus* and the posterior arm of the protoconid is absent. Enamel in the talonid basin is slightly wrinkled.

The small dP_4 (Fig. 2A) that has been referred here has a trigonid very different from that in *A.*

crepaturus, lacking both the anterior lophid between protoconid and metaconid and the posterior arm of the protoconid, and having a narrower trigonid basin that is open both anteriorly and posteriorly. There is a crest from the posterolingual side of the metaconid to the entoconid, which is more cuspate than in *A. crepaturus*.

A tentative assignment to *Anatoparamys* sp. is based on the open talonid basin that has no trace of a hypolophid.

Ischyromyidae taxon 1

Specimens.—Left dP^4, IVPP V 11037.1; left $M^{1 \text{ or } 2}$, V 11037.2.

Locality.—Fissure B.

Description.—Two heavily worn upper teeth from fissure B represent a taxon different from others at Shanghuang. A wider buccal than lingual side characterizes the dP^4 (Fig. 2D), which has an anteroposteriorly elongated protocone and no hypocone. The protoloph extends nearly transversely between protocone and paracone, whereas the metaloph is inclined more anterolingually. A thickening on the metaloph suggests presence of a metaconule. $M^{1 \text{ or } 2}$ (Fig. 2E) is more square in outline than dP^4. Both weak lophs of $M^{1 \text{ or } 2}$ are transversely oriented; an elongated thickening on the metaloph suggests a single or double metaconule.

Although different from *Anatoparamys*, the weak lophs and elongate protocone suggest that this poorly known taxon may be a member of the same clade of ischyromyids.

Ischyromyidae taxon 2

Specimens.—Right $M^{1 \text{ or } 2}$, IVPP V 11036.1; right M^2, IVPP V 11036.2.

Locality.—Fissure B.

Description.—Two upper molars represent the largest rodent taxon from the Shanghuang fissures. IVPP V 11036.1 is so worn that the occlusal surface shows very little detail. The second tooth, IVPP 11036.2 (Fig. 2F) is slightly worn, and its wider trigon than talon suggests that it is an M^2. It has rounded cusps and very weak lophs. The large protocone is anteroposteriorly elongate, occupying the entire lingual wall of the tooth, and there is no trace of a hypocone. From the paracone, the most prominent cusp, a narrow loph extends lingually to intersect a wider loph from the protocone, together forming a protoloph on which there is no trace of a protoconule. A distinct rounded mesostyle is slightly elongated transversely. The metacone, which is set well forward, contacts a large rounded metaconule, which is doubled by a rounded buccal bud that extends into the valley between the metacone and the narrow posterior cingulum. Even in this rather worn tooth, there is no loph from the larger metaconule to the protocone. Both upper molars are slightly unilaterally hypsodont.

Ischyromyidae taxon 3

Specimen.—Left $M^{1 \text{ or } 2}$, IVPP V 12667.

Locality.—Fissure A.

Description.—This upper molar is close in size and morphology to M^2 of *A. crepaturus* except that it has the following: an anteroposteriorly wider anterior cingular shelf; a long, narrow, complete metaloph lacking any trace of a metaconule and curving anterolingually to contact the protocone; and a second loph from metacone to protocone between the metaloph and the posterior cingulum. These features are important enough to preclude assignment to the species *A. crepaturus*.

DISCUSSION

Ischyromyids are a relatively rare part of the rodent assemblages from the Shanghuang fissures, in which they are exceeded somewhat in abundance by members of the ctenodactyloid family Yuomyidae but greatly outnumbered by the small cricetid *Pappocricetodon* (Wang and Dawson, 1994). Two ischyromyid

taxa are known from fissures D-E, *Anatoparamys crepaturus* and *Anatoparamys* sp. More poorly known are one taxon from fissure A, and two from fissure B.

Anatoparamys is marked by its bunodont, nearly non-lophate cheek teeth. Its occlusal pattern appears to be in the process of simplification, in a direction somewhat reminiscent of that of sciurids.

The poorly represented ischyromyid taxa 1 and 2 from deposits of fissure B resemble *Anatoparamys* in several characters. In both, the elongated protocone and absence of a hypocone are also features of *Anatoparamys*. Taxon 2 further resembles *Anatoparamys* in roundness of cusps and weakness of lophs. It appears to be more derived than the taxa from fissures D and E in having carried the bunodonty even farther and adding a doubled metaconule to fill the posterobuccal valley. Taxon 1 appears to have developed a rather different pattern, with narrow but more complete transverse lophs. The evidence for the affinities of these taxa is slight, but relationships with *Anatoparamys* may be supported by the morphology of the lingual wall of the upper molars. Other faunal evidence as well as the seemingly more derived character of these two taxa indicate a slightly younger age for Fissure B than for fissures D and E.

Fossils from fissure A are not abundant enough to establish its age relative to those of the other fissures, and the sole ischyromyid taxon from there is too poorly known to permit more than a tentative taxonomic assignment, although this taxon also has several hallmarks of the same clade as *Anatoparamys* (elongate protocone, bunodonty).

The distinctive dental characters of *Anatoparamys crepaturus* suggest that this may represent an endemic lineage of ischyromyids, possibly reflecting provincialism that is also demonstrated by other parts of the Shanghuang mammalian faunas (Qi et al., 1996). The fissures also contain indications, in the four less well-known rodent taxa, *Anatoparamys* sp. and three other taxa of ischyromyids, that this is a clade that had undergone some adaptive radiation in coastal southern China. In simplification of the molar patterns this clade shows similarities, probably homoplasies, to the North American manitshines and to some paramyines (Korth, 1985), most of which are, however, much larger rodents as well as having a different basic molar morphology.

A diet of soft vegetation for *Anatoparamys* and the other Shanghuang ischyromyids is suggested by their bunodont dentition. The considerable diversity of small primates, at least five species (Beard et al., 1994), and insectivores (Qi et al., 1996) preserved with the ischyromyids in the fissures is evidence supporting the interpretation of the Eocene environment around the exposed limestones as being a warm, forested ecosystem. In such surroundings, soft fruits and tender leaves were probably readily available as a diet for the ischyromyids and other small herbivorous mammals.

It is likely that predators, particularly birds, were responsible for a large part of the accumulations of dental and skeletal elements of the smaller vertebrates preserved in the fissure deposits. The small rodent *Pappocricetodon* was probably a prime target for these predators, but the larger yuomyids, which are in the size range of all but the largest ischyromyids, were also sampled with some frequency. Thus, the relative scarcity of ischyromyids in the fissure deposits probably reflects a low frequency of occurrence of the ischyromyids in the surrounding ecosystem.

So far as known, ischyromyids were not dominant in Asian Eocene faunas, whereas at that time they were more diverse and abundant in North America. The dominant Asian early and middle Eocene rodents were the ctenodactyloids (Tong,

1997; Dashzeveg and Meng, 1998; Guo et al., 2000). Somewhat later, starting in the later Middle Eocene, there began to be an increased diversity of cricetids and zapodids. Persistence of the ctenodactyloids in northern parts of Asia into the Oligocene and earlier Miocene was probably indicative of relatively dry ecosystems (Wang, 1997), an environment that appears to have been inimical to ischyromyids in Asia.

ACKNOWLEDGMENTS

Thanks are extended to our colleagues Qi Tao and Guo Jianwei (IVPP), Chris Beard (CMNH), Wang Qingqing and Di Fubao (Liyang Cultural Museum), and Ross MacPhee (AMNH), for taking part in the field work in the Shanghuang Quarry. Malcolm C. McKenna (AMNH) provided specimens for comparative purposes. Special thanks go to the numerous patient volunteers who sorted the immense volume of fossiliferous Shanghuang matrix at both the IVPP and CMNH. This project was supported by grants from the U.S. National Science Foundation (grant SBR 9221231), the Chinese National Science Foundation (grant no. 49372070), and the M. Graham Netting and Edward O'Neil funds of Carnegie Museum of Natural History.

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